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4.1.9 Feeding in Conodonts and other Early Vertebrates

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Introduction

Hypotheses of feeding are intimately bound up with scientific accounts of the early evolutionary history of vertebrates. The origin of vertebrates (= craniates), for example, has been linked to an ecological shift from suspension feeding to active predation, and changes in feeding mechanism are also invoked in various scenarios that seek to explain the origin of gnathostomes (vertebrates with jaws) from among the agnathans (jawless vertebrates) (see references in Purnell 1995; Pough *et al.* 1996). Competition for food resources has also been invoked to explain the decline of agnathans and the rise of jawed vertebrates (see Pough *et al.* 1996). Feeding in early vertebrates, however, is not well understood.

The Agnatha is a paraphyletic grouping of jawless fish (see Section 1.3.2), including anaspids, arandaspids, astraspids, conodonts, galeaspids, hagfish, heterostracans, lampreys, osteostracans, pituriaspids, and thelodonts (see Janvier 1996); the armoured members of this group are often referred to as ostracoderms. Except for lampreys and hagfish, all agnathans are extinct, and direct observation of feeding is not possible. The functional analysis of organisms known only as fossils must be based on comparisons with living organisms, and in many cases these comparisons ultimately depend on an hypothesis of homology at some level. But where relationships and homology are unknown or poorly constrained, hypotheses of function may rest entirely on analogy. Unfortunately, functional hypotheses based on analogy are difficult to test and may be little more than speculation. This has hampered the understanding of feeding in extinct agnathans: they were jawless, but possessed a variety of oropharyngeal feeding structures (e.g. the phosphatic elements of the conodont apparatus,

the oral plates of heterostracans and osteostracans, and the mandibular plate of anaspids) which lack homologues in extant taxa. Consequently, hypotheses of feeding have ranged widely, with little evidence of a consensus emerging.

Feeding in conodonts

Until quite recently, feeding in conodonts was probably less well understood than in any other group of fossil agnathans. Now that the agnathan affinities of conodonts are known (see Section 1.2.4), however, analysis of the function of their phosphatic elements and their feeding mechanisms has taken on new significance for understanding the early evolution of vertebrates. From the evidence of the few specimens that preserve remains of conodont soft tissues, it is clear that the elements were located in the oropharyngeal region of the head. Natural assemblages preserving elements in their original, but flattened, arrangement indicate that they formed a bilaterally symmetrical array. There is no longer any dispute that this apparatus was involved in feeding, but what is more contentious is whether it formed a suspension-feeding structure, or functioned as a set of teeth. Both these hypotheses are supported by analogies with living organisms, but the elements lack homologues among extant taxa. Nor was the debate regarding function resolved by the discovery of soft-tissue remains of conodonts (see Purnell 1999). However, testable predictions of apparatus growth rates can be derived from hypotheses of function. If the conodont apparatus formed a filtering device, the food intake of the animal would have been dependent on the surface area of the filtering array formed by the anterior elements of the apparatus, and in an isometrically growing animal this would have increased in proportion to body mass to the power 0.67. Food requirements, however, are linked to metabolic rate, which increases in proportion to body mass to the power 0.75. Thus, the increasing metabolic demands of a growing conodont would require positive allometry of the elements involved in filtering. No taxa for which apparatus growth rates have been analysed quantitatively exhibit positive allometric growth (see Purnell 1999). This indicates that conodonts were not suspension feeders.

This test may be quantitative, but it is none the less inferential, and relies on certain assumptions regarding conodont growth (Purnell 1999). However, direct evidence of feeding in conodonts has been obtained from the analysis of wear and surface damage on conodont elements. Damage to feeding structures produced during their normal use provides a fundamentally different type of evidence to that obtained from functional analysis of morphology. For fossils such non-structural evidence represents the closest approximation to direct

observation of function (Purnell 1999). Of particular significance in conodonts is the development of microwear textures within wear facets on functional surfaces (Fig. 4.1.9.1). These are comparable to the microwear textures developed on the teeth of mammals, and allow precise characterization of feeding in conodonts. The smooth, polished areas on the blade of *Gnathodus bilineatus* (Fig. 4.1.9.1a), for example, indicate either that this part of the element was in contact with the opposed blade without intervening food, or more likely that the species ate food that was not abrasive. The pitted microwear on *Idiognathodus* platforms (Fig.

4.1.9.1b) indicates that food was crushed between opposed elements, but the lack of associated scratches indicates that they did not grind. The parallel scratching on elements of *Ozarkodina confluens* (Fig. 4.1.9.1c) and *Drepanoistodus* (Fig. 4.1.9.1d) is diagnostic of shearing. The scratching reflects the abrasiveness of the food consumed, and it is probable that *Drepanoistodus* ate food that contained more abrasive particles than the food of *O. confluens*. Also, the degree of parallelism of scratches on teeth reflects the tightness of occlusal guidance, and given that conodonts were jawless, suggests surprisingly precise control of element motion and contact. This

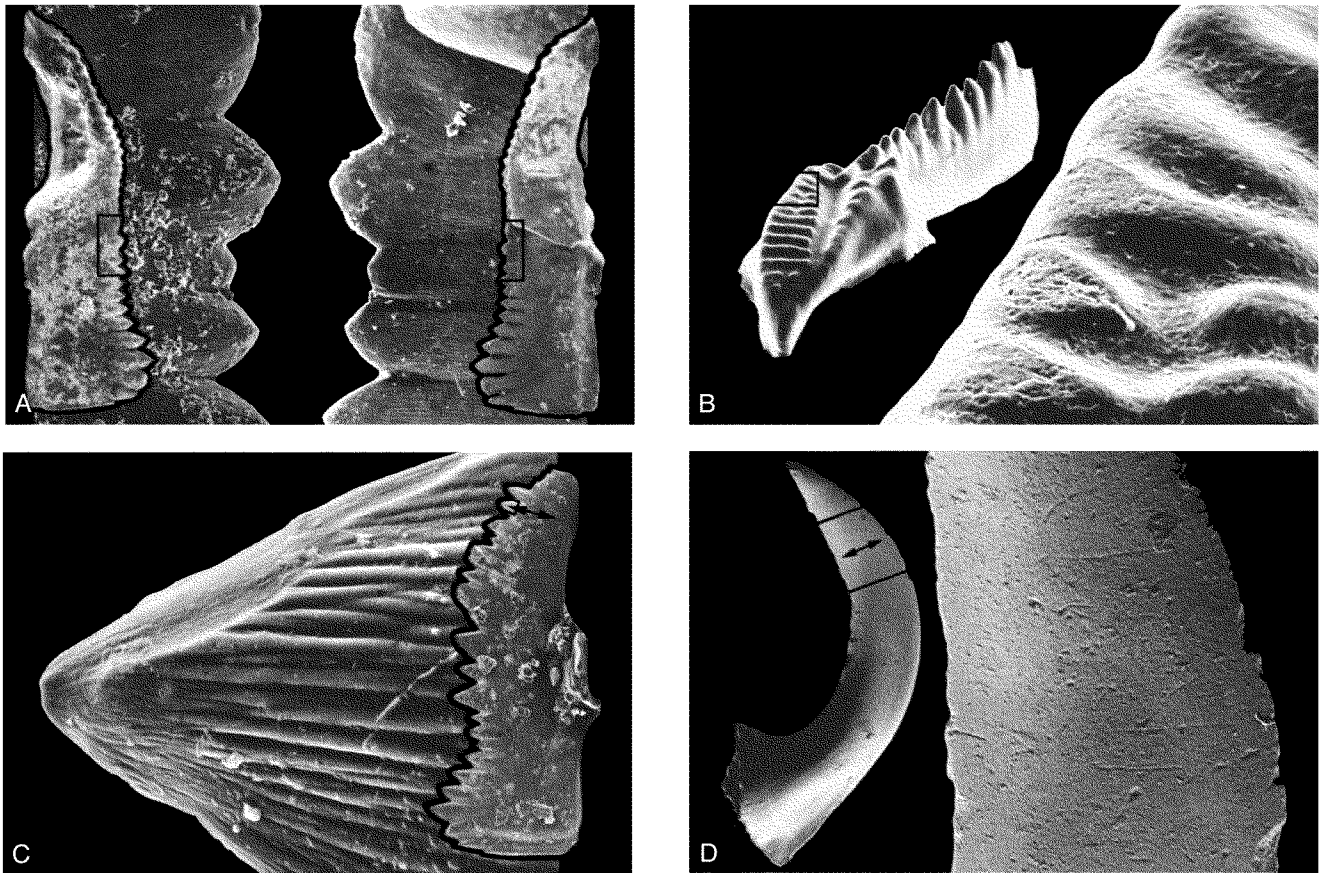


Fig. 4.1.9.1 Microwear in conodont elements. (a) Pa element of *Gnathodus bilineatus* (Carboniferous, UK); the original fibrous surface texture is well preserved on the anterior surface of the element (shown on left) but has been worn off the posterior surface (shown on right) where it was in contact with the opposed element; this wear, on one side only, cannot be the result of postmortem abrasion; whole element $\times 26$, close-up $\times 208$. (b) Pa element of *Idiognathodus* (Carboniferous, USA); the crests of the platform ridges in this element are blunted and flattened to form triangular wear facets with pitted microfeatures; such features are not developed elsewhere on the element and are most unlikely to be postmortem artefacts; whole element $\approx \times 33$, close-up $\approx \times 350$. (c) Pa element of

Ozarkodina confluens (Silurian, UK); a well-developed wear facet formed by contact with the opposed element sharply truncates the original fibrous surface texture; the facet is covered with fine, parallel striations (arrows indicate orientation of shearing motion); the distinctive nature of this facet and its location, between denticles, preclude a postmortem origin; whole element $\times 35$, close-up $\times 1227$. (d) Element of *Drepanoistodus* (Ordovician, Saudi Arabia), apex tilted a little towards viewer; a number of straight, parallel scratches traverse the slightly convex surface; their parallelism precludes a postmortem origin (arrows indicate orientation of shearing motion); whole element $\approx \times 33$, close-up $\approx \times 174$. (After Purnell 1995; © Macmillan Magazines Ltd.)

applies even to *Drepanoistodus*, which bore only simple cone-shaped elements and belongs to a primitive order of the Conodonta dating back to the Late Cambrian. The broader significance of shearing for hypotheses of feeding lies in the fact that it represents a method of food breakdown that is incompatible with microphagy, thus providing unequivocal evidence that conodonts were macrophagous.

Food processing in conodonts can now be analysed in detail based on wear and surface damage, but hypotheses of food acquisition are, as yet, unsupported by such direct evidence. The skeletal architecture of ozarkodinid conodonts, however, provides some new physical constraints derived from the spatial arrangement of the elements (Purnell and Donoghue 1997). This work suggests that the comb-like S and M elements at the anterior of the apparatus were attached to a pair of cartilaginous dental plates, similar to those of extant agnathans, and that when in use these plates were pulled forwards and pivoted over the anterior edge of an underlying ventral cartilage. The resulting anterior and ventral motions opened the apparatus; grasping was brought about by the reverse action, producing a net posterior and inward rotation of the elements, as indicated by the arrows on Fig. 4.1.9.2. This motion need not have been a steady, smooth action; as the dental plates pivoted over the anterior edge of the underlying cartilage the apparatus may have snapped back into the closed position, in a manner similar to closure of the hagfish lingual apparatus. This hypothesis of grasping was based on a detailed architectural model of the ozarkodinid apparatus, but it is probably also applicable to other groups of conodonts

with comparable spatially differentiated apparatuses, such as prioniodinids and prioniodontids. These groups represent fairly derived conodonts, however, and although food acquisition in primitive coniform taxa may have involved a similar mechanism of closure, the details are currently unknown.

Hypotheses of feeding in other early vertebrates

Although a bilaterally operating feeding apparatus is a synapomorphy of vertebrates (Purnell and Donoghue 1997), there is no evidence that any other extinct agnathans possessed an eversible feeding apparatus. Similarly, there is no evidence to support the hypothesis that the conodont apparatus is directly comparable to the oral or pharyngeal structures of ostracoderms. In fact, these structures have not been subjected to rigorous functional analysis and, apart from the conodonts, hypotheses of feeding in extinct agnathans are poorly constrained and generally speculative. Evidence from the few specimens that preserve gut contents is inconclusive, and some hypotheses are based on nothing more than gross body shape and inferred mode of life (see Janvier 1996). Many mutually exclusive alternatives have been proposed, and hypotheses of feeding in heterostracans and anaspids, just two groups of agnathans, provide a good illustration of the problem. Published interpretations include predation (with or without rasping tongue), mud grabbing, microphagous suspension feeding, deposit feeding, algal frond snipping or scraping, plankton feeding, detritivory, and suction

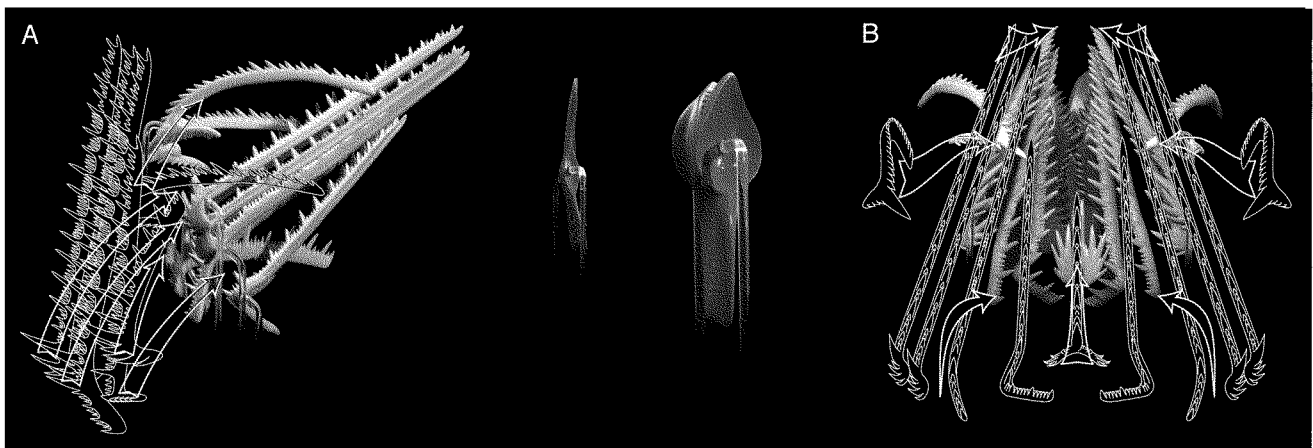


Fig. 4.1.9.2 Hypothesis of grasping by anterior elements of ozarkodinid apparatus. Elements drawn in outline indicate their position when the apparatus is everted and open; photographs show elements in the retracted position. (a) Lateral view of apparatus; arrows indicate net movement of

the S and M elements during retraction and closure of the anterior array. (b) Anterior view of apparatus; arrows indicate net movement of S and M elements. (After Purnell 1999; modified from Purnell and Donoghue 1997.)

feeding. Some of these hypotheses are contradicted by what is known of the biology of agnathans; suction feeding, for example, is difficult to reconcile with evidence that without jaws agnathans were unable to generate strong suction (Purnell and Donoghue 1997). Other modes of feeding are at least possible but have yet to be tested thoroughly.

So, what are the implications for scenarios of early vertebrate evolution? The evidence that conodont elements functioned as the teeth of a primitive macrophagous vertebrate supports hypotheses that the first vertebrates were predators. Without more rigorous analysis of feeding in other extinct agnathans, however, hypotheses which link the evolutionary history of the early jawless vertebrates to changes in feeding mechanism or to competition from gnathostomes must be viewed as speculative.

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